

DOES THE LARGE BARNACLE *AUSTROBALANUS IMPERATOR* (DARWIN, 1854) STRUCTURE BENTHIC INVERTEBRATE COMMUNITIES IN SE AUSTRALIA ?

ANDREW R. DAVIS AND DAVID W. WARD

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The shallow subtidal zone of SE Australia is dominated by urchin-grazed barrens, created and maintained by a large urchin, *Centrostephanus rodgersii* (A. Agassiz). We sought to determine how benthic invertebrates, such as sponges and colonial ascidians, maintain space in the face of this intense grazing pressure. Our data indicate that the cover of invertebrates on vertical substrata was positively correlated with the density of a large barnacle *Austrobalanus imperator* and are consistent with this barnacle providing a refuge from urchin grazing. The exception was the common sponge *Clathria pyramida* which showed a strong negative relationship with barnacle density. We speculate that as aggregations of barnacles may represent foci for competitive interactions among sessile invertebrates, *C. pyramida* seeks to avoid these sites. It appears that recruitment of *A. imperator* is sporadic and hence the conditions which allow the establishment of high densities of this barnacle remain unclear. As our data are correlative they must be interpreted cautiously. Experimental manipulation of barnacle density will provide a much clearer indication of the role of *A. imperator* in structuring these communities and is the focus of current work. □ *Porifera*, *Crustacea*, *Echinodermata*, *grazing refugia*, *structural habitat complexity*, *urchin grazing*, *Clathria pyramida*.

Andrew R. Davis (email: andy_davis@uow.edu.au) & David W. Ward, Australian Flora and Fauna Research Program and Department of Biological Sciences, University of Wollongong, NSW, 2517, Australia; 15 March 1999.

On subtidal rock walls, sessile invertebrates, such as sponges and ascidians, may cover a substantial area of the substratum. Typically in these communities habitable space is at a premium and competition for this resource is frequently intense. The loser in these spatial interactions is usually overgrown and killed. In addition to the intense spatial interactions characteristic of these communities, it is also clear that the action of predators (we use the term in its broadest sense and include grazing sea urchins) can have dramatic effects on community structure and dynamics. Urchins are capable of completely removing encrusting invertebrates and fleshy algae, thereby producing a community dominated by crustose algae (Lawrence, 1975; Vance, 1979; Ayling, 1981; Sebens, 1985; Witman, 1985).

Some organisms can resist grazing by urchins and may provide refuges for less resistant species. Several studies have stressed the importance of refugia from urchin grazing in determining the structure of algal (e.g. Dayton, 1985) and invertebrate communities (e.g. Witman, 1985). For example, encrusting communities in the rocky subtidal of New England, USA, reach

their greatest profusion either in the absence of urchins, or within beds of the mussel *Modiolus modiolus* when urchins are abundant (Sebens, 1985, 1986; Witman, 1985). This large bivalve adds significantly to the structural complexity of these rock wall habitats and serves as an important refuge for organisms against grazing urchins and predators (Witman, 1985; Ojeda & Dearborn, 1989). Structural habitat complexity may not only modify the foraging activities of predators it may also influence the settlement and recruitment of marine invertebrates (Keough & Downes, 1982).

An examination of the structure of rock wall assemblages, must therefore consider the potential for grazer-resistant species (such as *Modiolus*) to form refuges, both from grazing and the activities of other predators. On the other hand, refuge forming species will take up space - a limiting resource - and may thus be in direct competition with those species that do not require a refuge. The expectation is then, that some species will be positively associated with refugia, while other species will be negatively associated.

On the New South Wales (NSW) coast the sea urchin, *Centrostephanus rodgersii*, is the most



FIG. 1. A, The sponge *Darwinella australiensis* with a clump of *Austrobalanus imperator* as the urchin *Centrostephanus rodgersii* lurks nearby (Photo A. Davis). B, A high density of *A. imperator* overgrown by the sponge *Tedania* sp. Only the opercular plates of the barnacles are visible (Photo D. Ward).

conspicuous generalist grazer in the shallow rocky subtidal zone. This urchin creates and maintains extensive areas of substratum dominated by grazer-resistant encrusting coralline algae (Fletcher, 1987; Andrew, 1991). In these urchin grazed areas, sponges and colonial ascidians, reach their greatest profusion on rock walls or the vertical faces of large boulders. The large barnacle *Austrobalanus imperator*, which can measure over 4cm in height, also forms dense aggregations on shallow subtidal rock walls (Davis & Ward, unpublished data), thereby adding significantly to the structural complexity of these habitats (Fig. 1A). Another barnacle, *Balanus trigonus*, also often occurs in high densities in the subtidal zone, but is relatively small.

As part of a study to examine determinants of the structure and dynamics of natural rock surfaces in SE Australia we sought to determine how sessile invertebrates might maintain space in the face of intense grazing pressure by sea urchins. The sheer size of *A. imperator* combined with the high densities that occur on some rock walls should, we reasoned, represent a significant hinderance to grazing urchins and for that reason these barnacles are likely to play an instrumental role in determining the structure of subtidal rockwall communities. We initiated this study by collecting quantitative data on the relationship between invertebrate cover and the density of *A. imperator*.

MATERIALS AND METHODS

The relationship between barnacle density and invertebrate cover was investigated at three sites on the S coast of NSW. Sites were selected to encompass a length of the coast and for their convenient access. From north to south the sites were Henry Head (34°0.0'S, 151°14.2'E) at the N entrance to Botany Bay, the N end of Flinders Islet (34°27.3'S, 150°55.7'E) near Wollongong, and Longnose Point (35°4.5'S, 150°47.0'E) within Jervis Bay (Fig. 2). These sites spanned almost 150km of coastline and we considered them representative of a much larger number of potential sites. Vertical surfaces, ranging from rock walls to the faces of large boulders were haphazardly photographed at all sites, usually between a depth of 5-15m. A camera (Nikonos V), mounted on a frame with twin strobes (Nikonos SB102 and Ikelite Ai strobes) to provide even illumination, produced photographs of an area of 0.08m². Between 24-36 haphazard photographs were taken at each site after applying the criterion that the surface was vertical or near vertical.

The total cover of invertebrates was estimated from the photographs using a transparency overlay with 100 systematically arranged dots. Only sessile invertebrates were considered and so the anemone *Anthothoe albocincta*, although

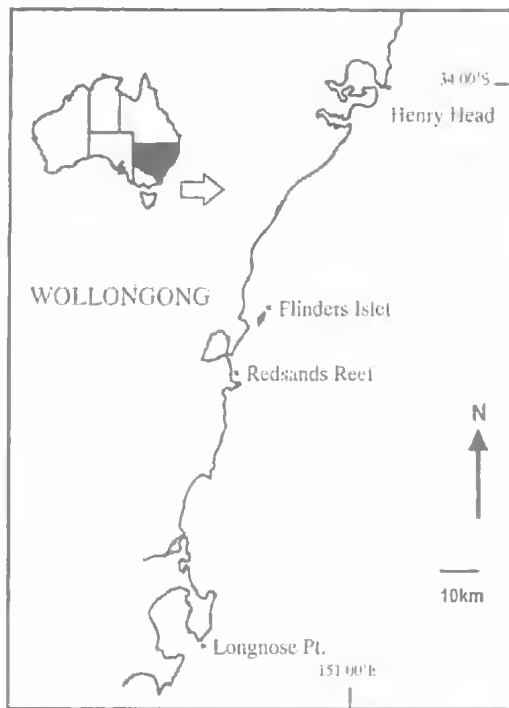


FIG. 2. Study sites on the S coast of NSW, Australia. The relationship between invertebrate cover and barnacle density were assessed at Henry Head, Flinders Islet and Longnose Point. The size frequency of *Austrobalanus imperator* was determined at Flinders Islet and Redsands Reef.

quite common in some areas was excluded owing to its mobility. The number of barnacles was also counted on each photograph. We were initially concerned that barnacles may be obscured by overgrowth, but found no evidence of this; the opercular plates of *Austrobalanus imperator* were always visible (Fig. 1B). Barnacles down to a size (basal diameter) of 5mm could be reliably recorded from the photographs. Correlation coefficients (Pearson) were calculated for each site.

Close examination of the photographs indicated that the pattern of distribution of one sponge, *Clathria pyramida*, contrasted with that of the other sessile invertebrates. To better assess the relationship between this sponge and the barnacles a series of haphazard photographs were taken of *C. pyramida* at Flinders Islet in September, 1995. Sponge cover was again estimated using the overlay transparency on the photographs and barnacles were also counted and recorded.

In order to get a clearer picture of the potential of *A. imperator* to form a refuge from urchin grazing we determined the size frequency of this barnacle at two sites; Flinders Islet and Redsands Reef ($34^{\circ}35.7'S$, $150^{\circ}54.3'E$, Fig. 2). The maximum diameter of the base of each barnacle was measured in the field with calipers. To ensure that basal width was a good estimator of barnacle tissue bioass we regressed barnacle tissue dry weight against basal width. Data were pooled from collections at Flinders Islet and Redsands Reef.

RESULTS

Clathria (Dendrocia) pyramida Lendenfeld (Porifera, Demospongiae, Poecilosclerida, Microcionidae), showed a significant negative relationship with the density of the barnacle *A. imperator* ($r=-0.54$, $n=24$, $P<0.05$, one tailed test, Fig. 3). In contrast, the total cover of invertebrates, excluding *C. pyramida*, was strongly positively correlated with barnacle density at all three sites. Barnacle density explained more than 30% of the variation in invertebrate cover at two of these sites, Henry Head ($r=0.548$, $P<0.001$) and Flinders Islet ($r=0.586$, $P<0.001$). The positive relationship between barnacle density and cover of invertebrates was not statistically significant by a one tailed students t-test at Longnose Point

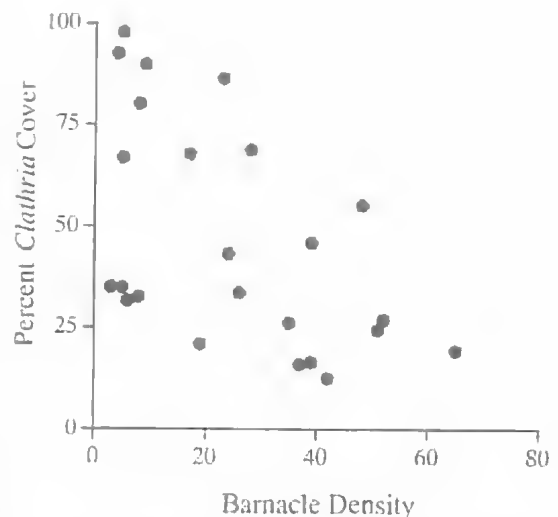


FIG. 3. The cover of *Clathria pyramida* was negatively correlated with the density of the barnacle *Austrobalanus imperator* within photographic plots. Each data point represents a plot photographed on 13 September, 1995 at Flinders Islet. ($r=-0.54$, $n=24$, $P<0.05$, one tailed test).

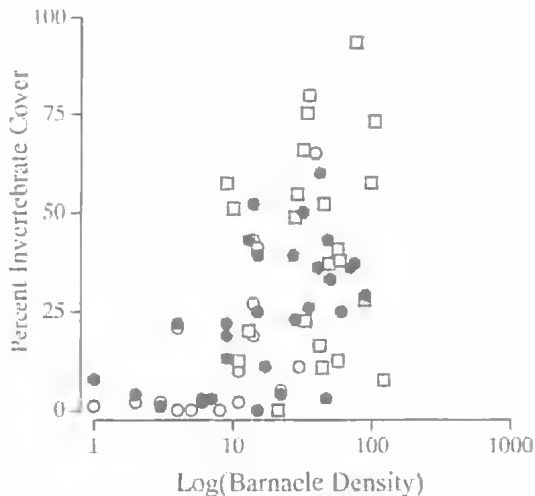


FIG. 4. Positive correlation between total invertebrate cover (excluding *Clathria pyramida*) and the density of the barnacle *Austrobalanus imperator* within photographic plots. Each data point represents a plot photographed at Henry Head (solid circle), Flinders Islet (open circle) and Longnose Point (square). All tests of significance were one tailed tests, Henry Head ($r=0.548$, $P<0.001$), Flinders Islet ($r=0.586$, $P<0.001$) and Longnose Point ($r=0.107$, $P>0.05$).

($r=0.107$, $P>0.05$). We present the data with the barnacle density log transformed to provide a more even spread of data on the x axis (Fig. 4).

The modal size of adult barnacles at both sites was between 35–40 mm, with the largest individuals having a basal width of around 55 mm. Recruits of *A. imperator* were not recorded at either site from which we collected size frequency data. A cohort of 'sub-adults' were observed at the Redsands Reef site, but these animals were still quite large with a modal basal width of around 15 mm (Fig. 5A). No such cohort was observed at the Flinders Islet site (Fig. 5B). Maximum basal width of the barnacles was an excellent estimator of animal biomass (Fig. 6). The resultant power function produced a very strong correlation ($y=0.0000069x^{3.043}$, $r=0.95$).

DISCUSSION

With increasing densities of barnacles the cover of sessile invertebrates was also seen to increase. These findings are consistent with our initial suspicion that aggregations of *Austrobalanus imperator* form a refuge from sea urchin grazing. The rocky intertidal provides several examples of how habitat structure

influences the activities of grazers (Hawkins & Hartnoll, 1982; Cresc. 1982; Dungan, 1986). For example, Creese (1982) reported that surface heterogeneity provided by barnacle shells can markedly influence the ability of grazers to feed. Limpets caged with high densities of a common intertidal barnacle starved to death (Creese, 1982).

In addition to modifying patterns of invertebrate mortality, habitat structure may influence patterns of invertebrate colonisation. Bros (1987) reported a positive relationship between invertebrate recruitment and the addition of barnacle shells to glass slides in Tampa Bay Florida, although he noted that the treatments did not greatly affect the colonisation of sessile species. The responses of colonists to the modification of habitat structure on natural substrata remains unclear.

Although it is tempting to ascribe our findings to an increase in structural heterogeneity produced by the presence of these large barnacles an equally plausible alternate explanation is that the barnacles simply enhance recruitment rather

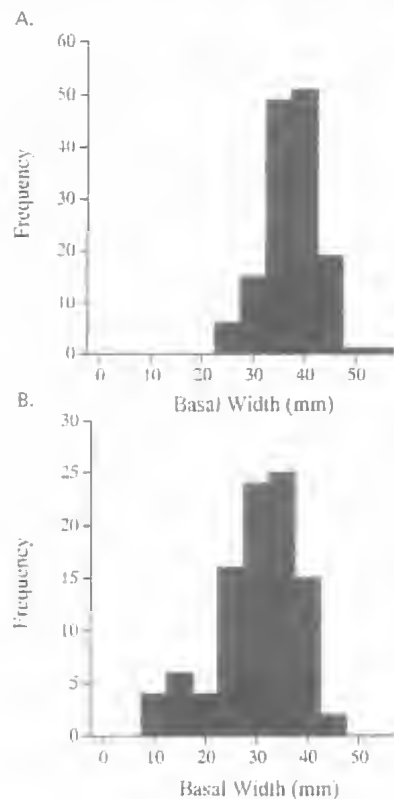


FIG. 5. Size frequency of *Austrobalanus imperator* at: A, Flinders Islet; and B, Redsands Reef. Data were collected on a single day in October, 1994 at each site.

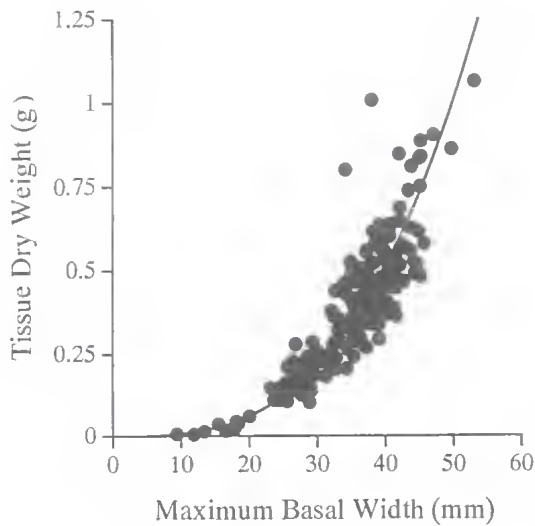


FIG. 6. Relationship between the maximum width of *Austrobalanus imperator* at their base with dry tissue weight ($r=0.949$).

than reducing mortality. Changes in hydrodynamics near the rock surface or the additional surface area provided by barnacles when compared to a smooth rock surface are two potential mechanisms by which invertebrate recruitment may be enhanced. Nevertheless our data are correlative and in the absence of experimental evidence we can only speculate as to the processes which have produced the patterns we have observed. Notably, though, we have produced a conservative test of our initial hypothesis as a high density of barnacles will leave less space for other sessile invertebrates, yet we see higher invertebrate cover in the presence of high densities of barnacles.

The striking negative relationship that we observed between barnacle density and the cover of *C. pyramida* suggests that this sponge is not reliant on the presence of barnacles to establish itself successfully and maintain space. *Clathria pyramida* clearly contains novel metabolites (Capon & Macleod, 1987) and field bioassays with crude solvent extracts of this sponge have revealed the presence of antifeedant natural products that dissuade urchins (*Centrostephanus rogersii*) from grazing (Wright et al., 1997). The nature of the deterrent metabolites is currently unknown, but is under investigation (Davis & van Altena, work in progress). It is likely that the presence of biologically active metabolite(s)

explains why this sponge does not rely on the presence of barnacles. However, the strong negative relationship we observed is consistent with the avoidance of barnacles by *C. pyramida*. This may be an appropriate strategy if this sponge is likely to encounter competitively superior species among aggregations of barnacles. Several studies reveal that some invertebrate larvae can detect competitive dominants and subsequently avoid sites where their survivorship is likely to be compromised (Grosberg, 1981; Davis, 1987). There is no need to invoke avoidance of barnacles or competitive dominants by the larvae of *C. pyramida* to explain the observed pattern; directional growth by adults could produce the same pattern. The reasons why *C. pyramida* avoids barnacles and the mechanisms used to do this remain speculative as nothing is known of the competitive ability of *C. pyramida* relative to other sessile species it is likely to encounter in SE Australia.

It appears that the presence of *A. imperator* is an important contributor to the structure and dynamics of encrusting communities on vertical surfaces in SE Australia. Unfortunately, little is known of the biology of this cirripede or the determinants of its distribution and abundance; of particular interest for example is how recruits of the barnacle withstand grazing by urchins. Our data reveal that recruitment of *A. imperator* is sporadic as we did not detect reliable recruitment to the barnacle population in the course of this study. There are also no data on the growth rates of this barnacle and therefore the time taken to reach a size that may interfere with the grazing activities of urchins, thereby forming a refuge. Experimental manipulation of the density of this barnacle is an important step in better understanding its role in these benthic communities and is the focus of current work.

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